

Behavioral interactions between black mudfish (*Neochanna diversus* Stokell, 1949: Galaxiidae) and mosquitofish (*Gambusia affinis* Baird & Girard, 1854)

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Abstract – The behavior of black mudfish (*Neochanna diversus* Stokell, 1949: Galaxiidae) and mosquitofish (*Gambusia affinis* Baird & Girard, 1854: Poeciliidae) was investigated in laboratory tanks. Black mudfish are indigenous to northern New Zealand, and mosquitofish are introduced; both species are sympatric in wetlands in the Waikato region. By comparing position, feeding rates and aggressive behavior of both species, we found that black mudfish were increasingly able to compete with mosquitofish as they grew from fry to adults. Mosquitofish were more aggressive towards mudfish fry and juveniles than were these two life stages towards mosquitofish, but adult mudfish were aggressive towards mosquitofish. Both small (18–24 mm total length (TL)) and large mosquitofish (25–36 mm TL) showed high aggression towards mudfish fry (13–18 mm TL), and fry were eaten by large mosquitofish. However, 3 interspecific differences appear to allow coexistence of these two species. Firstly, mudfish reproduce in winter, whereas mosquitofish reproduce in summer, resulting in mudfish fry being present when mosquitofish are at their lowest abundance. Secondly, mudfish can survive in seasonally dry habitats by aestivation, while mosquitofish cannot. Thirdly, adult black mudfish are nocturnal, whereas mosquitofish are primarily diurnal.

R. F. G. Barrier, B. J. Hicks

Department of Biological Sciences, University of Waikato, Hamilton, New Zealand

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B.J. Hicks, Department of Biological Sciences, University of Waikato, Private Bag 3105, Hamilton, New Zealand

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

New Zealand has 3 endemic mudfish species: the black mudfish, *Neochanna diversus* Stokell, 1949; the brown mudfish, *N. apoda* Günther, 1867; and the Canterbury mudfish, *N. burrowsius* Phillips, 1926. Mudfish belong to the Southern Hemisphere family Galaxiidae (Salmoniformes). The Canterbury mudfish is the rarest, and is restricted to a small area of the east coast of the South Island, but black and brown mudfish are more widespread (McDowall 1990). Black mudfish occur in the northern half of the North Island, and brown mudfish occur in the lower half of the North Island

and in the northwestern part of the South Island. The principal habitat of all mudfish species is wetlands. Large areas of wetland throughout New Zealand have been drained and converted to farmland, reducing the habitat available for all mudfish species (McDowall 1990).

Introduced fish also threaten the survival of mudfish. Mosquitofish (*Gambusia affinis* (Baird & Girard, 1854)) pose a special threat, because of their breeding potential, aggression, predation of fish larvae and extreme environmental tolerances (McDowall 1990). Though mosquitofish are short-lived, they mature rapidly and can produce three broods a year in New Zealand (Wakelin 1986).

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Their fertilization is internal, and females can retain viable sperm over winter. Fertile females can, therefore, re-establish populations in summer in the absence of males (Haynes 1993). Mosquitofish are known to eat fish eggs and larvae (Myers 1965) and have become the dominant fish near human habitation in parts of Australia (McKay 1984). Mosquitofish were originally introduced to New Zealand in 1931 as an experimental control for mosquitoes (McDowall 1990) and are well adapted to survive in wetlands in the warmer (northern) parts of the country.

The aim of this study was to compare the feeding, aggression and predatory behaviour of black mudfish and mosquitofish so as to evaluate the risk mosquitofish pose to black mudfish in the wild.

Material and methods

The mosquitofish and mudfish used in the trials were collected from two wetland sites in the Waikato region where fish were locally abundant (about latitude 37° 30' S, 175° 30' E). Fish were trapped in winter (May to October) using 5-mm mesh Gee minnow traps baited with cheddar cheese. Some wetland sites contained only damp mud during summer, prohibiting trapping. Traps were set between 1300 h and 1700 h one afternoon and retrieved and emptied between 0900 h and 1100 h the following morning, taking advantage of the nocturnal activity of black mudfish. The captured fish were transferred to the laboratory and treated for white spot and fin rot by placing them in a solution containing $167 \text{ g} \cdot \text{m}^{-3}$ of 100% formalin solution and $1\text{--}2 \text{ g} \cdot \text{m}^{-3}$ of malachite green for 1 h (Hawkins 1981).

Laboratory behavioral trials were conducted between 2 October and 12 December 1992. Fish were kept in 4 cubic-shaped 30-l glass tanks with 35-cm sides. Two tanks were used to acclimate the fish and 2 tanks were used for the actual experimental trials. Adult mudfish would not feed at first under high light conditions and required 2 weeks of acclimation to feed consistently under high light. Juvenile mudfish needed only 48 h to acclimate to feed under high light. The test tanks had horizontal lines dividing them into four 5-cm layers to enable positions of fish to be recorded. Water temperatures ranged between 19.0°C and 20.5°C over the course of the trials.

Trials were conducted at high and low light intensities. Lighting for the high-light-intensity trials consisted of a 40-W fluorescent light and 2 tungsten lamps with 40-W bulbs suspended 1 m above the tanks. The light was projected downward through 70% light-reduction shade cloth. Light intensity was measured at mid-water depth with a

Licor Quantum radiometer, model Li-185A, fitted with a Licor 2 Pye probe, which read on average $0.23 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The photoperiod was controlled by a timer to approximate day length for the time of year (11 h light, 13 h dark).

Lighting for low-light-intensity trials was provided by a photographic darkroom safelight with a 60-W pearl, tungsten-filament bulb and a Kodak Safelight filter 2. Spectral emission from this light source was $>640 \text{ nm}$ (Barrier 1993) and simulated near-dark conditions. The light source was located 45 cm from the trial tank, 10 cm above the bottom. The light reading in the tank at mid-water was $0.075 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. To observe fish under the low light intensity, an infrared image converter was used to enhance visibility. Prey used in the feeding trials were daphnia (*Daphnia carinata*) or brine shrimp (*Artemia salinus*). Brine shrimp were used only in the trials involving black mudfish fry, as daphnia were too large for fry to swallow.

Trials were conducted with 1) mudfish fry (13–18 mm total length (TL)), 2) mudfish juveniles (30–50 mm) and 3) mudfish adults (80–100 mm). Classification of sizes with stages of maturity was according to Thompson (1987). Size classes of mosquitofish were: 1) small mosquitofish: males 18–20 mm, females 22–24 mm; 2) large mosquitofish: males 25–27 mm, females 30–36 mm. For trials involving mosquitofish, 2 males and 2 females were used. The sex of mudfish was not determined. Each mudfish size class was tested against both small and large mosquitofish where possible, giving a maximum of six trials. Four fish of each species were used, except for controls using only 4 mudfish. Fish were observed through slits from behind a black plastic screen to prevent disturbance of fish.

Before a trial, mudfish and mosquitofish were acclimated to the test tank for 24 h, except for trials with mudfish fry, where the trial commenced 5 min after the mosquitofish were added. None of the fish were fed for the 24-h period before a trial. Trials lasted 20 min, and were divided into a 10-min period of observation of aggressive interactions (intention movements, chases and contact nips (Hartman 1965; Mason 1969)) before feeding, followed by the introduction of food, and a 10-min period of observation of feeding behavior. In starting the feeding part of a trial, live prey were emptied carefully into the tank with a small hand net, causing minimal disturbance to the fish. The position of fish and the number of prey eaten by species was recorded for each of the 4 levels in the tank. Prey capture was recorded for only one pair of fish, i.e., one mudfish and one mosquitofish, or just one mudfish in control trials. Fish position was recorded at 2-min intervals (i.e., 5 times) over

a period of 10 min, and prey capture was noted over the same 10-min period. The resulting observations of both fish position and prey capture were pooled at the end of each trial. Trials with mudfish alone served as a control. No control trials were used for mosquitofish alone as our primary concern was the impact of mosquitofish on mudfish behavior. The same procedure was used for both high- and low-light-intensity trials. Trials under low light intensity were conducted after the timer-controlled lights had been off for at least 30 min. Three replicate trials were carried out, with at least 24 h separating each trial to eliminate possible bias from food-satiated fish. Mudfish fry and small mosquitofish were not used in trials under low light intensity because their small size precluded accurate recording of position and prey capture.

Results

Interspecific aggression

Black mudfish of all 3 life stages (fry, juvenile and adult) moved slowly in comparison to mosquitofish. Mosquitofish were more aggressive towards mudfish than were mudfish towards mosquitofish (Table 1). Small mosquitofish showed high rates of aggression towards mudfish fry, with chase used most frequently. Large mosquitofish ate mudfish fry shortly after the mosquitofish were released into the trial tank. Large mosquitofish chased and nipped juvenile mudfish, whereas small mosquitofish were not aggressive towards juvenile mudfish. Mosquitofish (large and small) were not aggressive towards adult mudfish, which was the only size class of mudfish to show aggression towards mosquitofish. However, adult mudfish were more aggressive towards mosquitofish under low light than under high light intensities. Nipping was the most frequently used aggression by adult mudfish against mosquitofish.

Fish position and prey capture

Under high light intensity, black mudfish fry occupied the surface level of the tank due to small mosquitofish aggression (Fig. 1). No comparison could be made with large mosquitofish because they ate mudfish fry. Prey capture rates by mudfish fry were reduced by mosquitofish in all water levels except the surface. In the absence of mosquitofish, mudfish fry were relatively evenly distributed in all tank levels. Juvenile mudfish were also distributed relatively evenly in the tank in the absence of mosquitofish (Fig. 1) but were forced to adopt more benthic positions when tested with mosquitofish. Prey capture rates by juvenile mudfish were also reduced in surface and midwater levels by the presence of mosquitofish, the effect being more pronounced with large mosquitofish than with small ones. Adult mudfish occupied bottom positions under high light intensity and showed generally low rates of prey capture (Fig. 1). Mosquitofish had no effect on the position of adult mudfish, but depressed their prey capture rates slightly.

Under low light intensity and in the absence of mosquitofish, both juvenile and adult mudfish were evenly distributed between the surface and the bottom levels of the tank, avoiding the mid-water positions (Fig. 1). Prey capture rates by both juvenile and adult mudfish were highest at the surface. Positions of juvenile and adult mudfish were not affected by the presence of mosquitofish, but prey capture by juveniles were depressed at the surface and at the bottom.

The position of mosquitofish and their prey capture rates were also examined. In trials under high light intensity, small mosquitofish were fairly evenly distributed throughout the tank in the presence of mudfish fry but took most prey in the upper mid-water level (Fig. 2). Small mosquitofish in the presence of juvenile mudfish were also evenly

Table 1. Interspecific aggression between black mudfish and mosquitofish. Results from three replicate trials pooled. —: trial not possible as mosquitofish ate mudfish fry.

Light intensity	Trial	Mosquitofish aggression towards mudfish			Mudfish aggression towards mosquitofish		
		Intention movement	Chase	Contact nip	Intention movement	Chase	Contact nip
High	Mudfish fry and small mosquitofish	7	19	2	0	0	0
	Mudfish fry and large mosquitofish	—	—	—	—	—	—
	Juvenile mudfish and small mosquitofish	0	0	0	0	0	0
	Juvenile mudfish and large mosquitofish	3	8	7	0	0	0
	Adult mudfish and small mosquitofish	0	0	0	2	1	0
	Adult mudfish and large mosquitofish	0	0	0	1	0	0
Low	Juvenile mudfish and large mosquitofish	0	0	0	0	0	0
	Adult mudfish and large mosquitofish	0	0	0	3	2	5

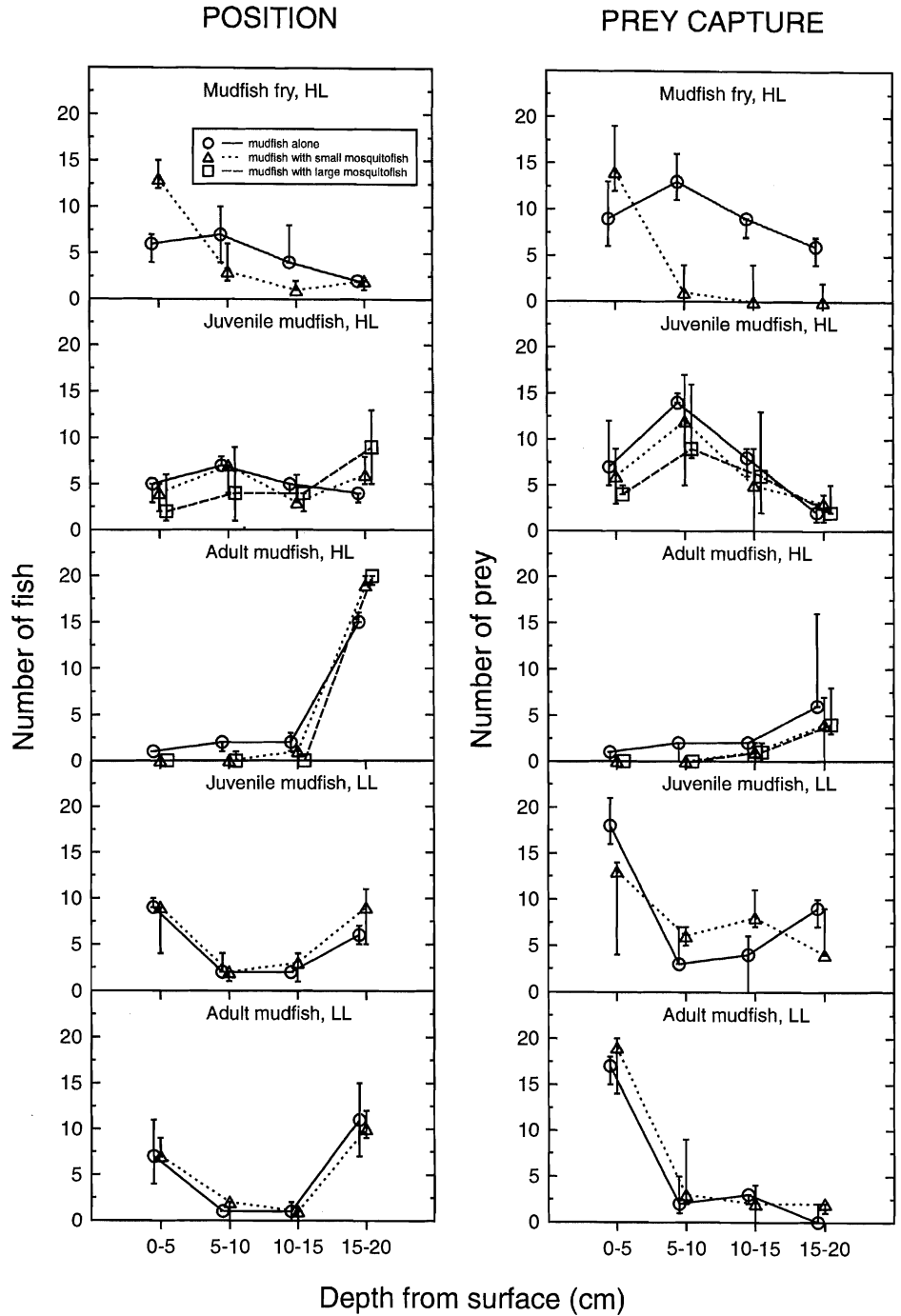


Fig. 1. Positions of mudfish and their prey capture rates in the presence and absence of mosquitofish in three 10-min trials under high (HL) and low light intensity (LL). Medians joined; bars represent extremes of three trials.

distributed throughout the tank, but took most of their food in the mid-water levels. However, large mosquitofish in the presence of both juvenile and adult mudfish appeared to concentrate in the lower water levels, where their prey capture rates were also highest. Small mosquitofish in the presence of adult mudfish were most commonly observed in the upper water levels, where their prey capture rates were highest, in contrast to the benthic orientation of large mosquitofish. Under low light in-

tensity, large mosquitofish with juvenile mudfish were benthic, but evenly distributed with large mudfish (Fig. 2).

Discussion

From the overseas literature, one might surmise that black mudfish would not compete successfully with the aggressive and prolific mosquitofish (Myers 1965; McKay 1984). Competition for plank-

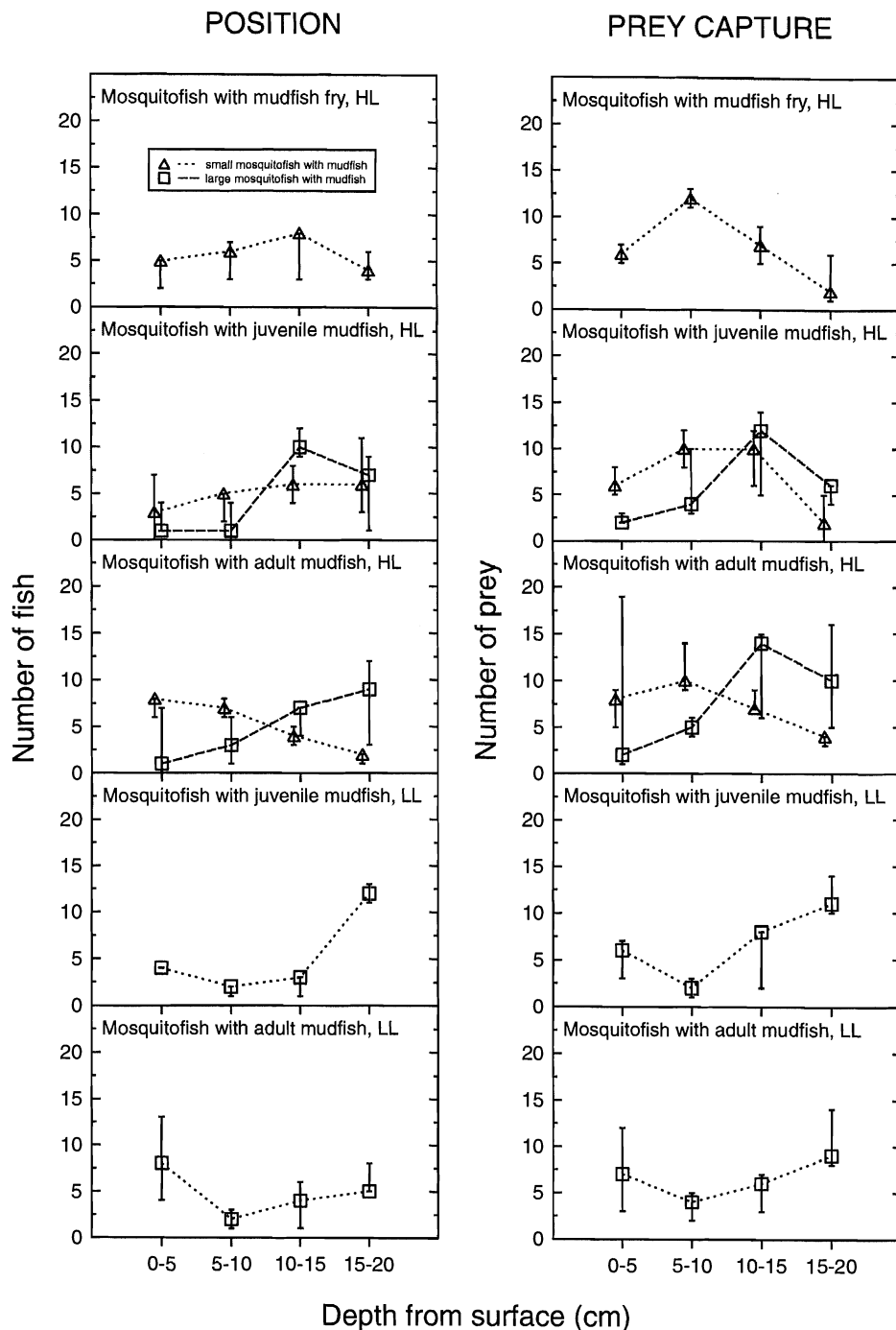


Fig. 2. Positions of mosquitofish and their prey capture rates in the presence of mudfish in three 10-min trials under high (HL) and low light intensity (LL). Medians joined; bars represent extremes of three trials.

tonic food almost certainly occurs, as mosquitofish can significantly alter the composition and abundance of zooplankton in small pools in summer (Hurlbert & Mulla, 1981). Zooplankton are important in the diet of black mudfish (Thompson 1987). However, mudfish in the Waikato region are capable of coexisting with mosquitofish (Barrier 1993). It appears that mudfish have adaptations that reduce their susceptibility to mosquitofish competition and predation. Winter breeding, sum-

mer aestivation and nocturnal activity may permit black mudfish to persist in spite of invasion of their habitat by mosquitofish.

Spawning in black mudfish and mosquitofish is temporally separated, effectively eliminating significant predation of mudfish fry by mosquitofish. Mosquitofish spawn only when water temperatures are above 16°C (Medlen 1951). The functional minimum for male reproductive activity is 16–18°C (Haynes 1993). In Lake Waahi in the Waikato re-

gion, Wakelin (1986) found that gravid females occur only in the warmest months (November to April). Spawning in black mudfish begins at the onset of winter rains, usually in June or July (Thompson 1987). During 9 years of observation of mudfish in the wild, Thomson found that larvae appeared between 28 April and 10 October. The greatest densities of fry 15–20 mm TL occurred between mid-August and mid-September. In 2.5 months, mudfish grew an average of 21 mm to 35–38 mm TL. Thus by the time water temperatures are sufficient for mosquitofish to breed, juvenile black mudfish are past the size where they can be preyed upon by mosquitofish.

Black mudfish have the ability to breathe air, surviving the drying of their habitat during summer droughts, whereas mosquitofish do not. We found two black mudfish (51 and 106 mm TL) in a dry drain near Hamilton City in mid-April 1993. These mudfish had not made burrows but were laying inactive on a sediment surface protected from excessive dehydration by a covering of damp vegetation (Hicks & Barrier, unpublished data). Aestivation is known in the brown mudfish and in the Canterbury mudfish (Eldon 1978, 1979), which make cocoons in mud, and has been inferred for black mudfish because of their relatedness to the other two species (McDowall 1990). Thus in summer, when competition with mosquitofish might be severe, black mudfish may occupy habitats that dry to damp mud or peat, covered with wetland vegetation (rushes, sedges and grasses). Mosquitofish cannot survive such conditions, so summer droughts, which are a regular feature of the areas inhabited by black mudfish, may limit populations of mosquitofish, and reduce competition with black mudfish. Recent experiments suggest that aestivation by black mudfish is a true metabolic adjustment to dry conditions. The oxygen uptake rate fell by about 80% within 24 h of the onset of dry conditions (N. Ling, University of Waikato, unpublished data). Despite this, our two aestivating mudfish regained activity immediately upon immersion in water.

Black mudfish fry are vulnerable to predation by mosquitofish. As mudfish fry are surface-oriented and diurnally active, mosquitofish pose a significant threat to their survival. However, mudfish fry quickly outgrow this vulnerable stage, and then undergo behavioral changes that may allow them to compete with mosquitofish. Larger mudfish are increasingly more benthic and more nocturnally active than their smaller counterparts. Though mosquitofish may affect the vertical distribution of juvenile mudfish in the water column and prey capture rates, the effects are less than for mudfish fry. Adult mudfish, on the other hand, are virtually unaffected in their vertical distribution or prey cap-

ture by the presence of mosquitofish. Moreover, the median prey capture rates by juvenile and adult mudfish is about 2–3 times that of mosquitofish under low light intensity (Fig. 2). Mudfish appear better adapted to nocturnal feeding, and under low light intensity they may outcompete mosquitofish.

In summary, sympatry between black mudfish and mosquitofish in the Waikato region may be largely attributed to 1) mudfish becoming increasingly nocturnally active as they grow, compared with diurnal activity in mosquitofish; 2) mudfish reproduction in winter, compared with mosquitofish reproduction in summer; and 3) mudfish survival in seasonally dry habitats by aestivation. Mosquitofish cannot aestivate. These traits may allow the slow-moving and relatively non-aggressive black mudfish to compete successfully with the invasive, aggressive and prolific mosquitofish.

Resumen

1. El Black Mudfish (*Neochanna diversus* Stokell) es un galaxido (fam. Galaxiidae) nativo del norte de Nueva Zelanda mientras que la Gambusia (*Gambusia affinis* Baird & Girard) es introducida y ambas viven en simetría en la región de Waitako (Nueva Zelanda).
2. Comparando las posiciones espaciales, tasas alimenticias y comportamiento agresivo en tanques experimentales, encontramos que los individuos de *N. diversus* fueron progresivamente más capaces de competir con los individuos de *G. affinis* al ir creciendo desde pos-larva hasta adulto.
3. Las gambusias fueron más agresivas hacia los estadios pos-larvarios y juveniles de *N. diversus* que estos dos estadios hacia las gambusias pero los adultos de *N. diversus* también fueron agresivos hacia las gambusias. Las gambusias, tanto pequeñas (18–24 mm Lt) como grandes (25–36 mm Lt) mostraron alta agresividad hacia las pos-larvas (13–18 mm Lt) de *N. diversus* que fueron comidas por gambusias grandes.
4. A pesar de ello, hay al menos, tres diferencias interespecíficas que parecen permitir la co-existencia entre ambas especies. Primero, *N. diversus* se reproduce en invierno mientras que las gambusias lo hacen en verano, resultando en que las poslarvas de *N. diversus* están presentes cuando las gambusias están en mínimos de abundancia. Segundo, en contraposición a las gambusias, *N. diversus* puede sobrevivir en habitats que se secan estacionalmente. Tercero, los adultos de *N. diversus* son nocturnos mientras que las gambusias son fundamentalmente diurnas.

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